OBSERVATIONS ON THE VERTICAL DISTRIBUTION OF *ORIBATEI* (*ACARINA*) IN TWO WOODLAND SOILS

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INTRODUCTION

The *Oribatei* are one of the dominant arthropod groups in temperate woodland soils and studies on their vertical distribution (VAN DER DRIFT, 1951 ; RHIA, 1951 ; WALLWORK, 1959 among others) have shown them to be predominantly associated with the superficial litter and humus layers of the profile. HAARLØV (1953) has described the decreasing size of soil cavities with increasing depth as limiting the distribution of soil Acari in relation to their body size. He stressed that this depth distribution must also be related to the feeding, temperature and humidity relationships of the individual species concerned. Many authors, notably RIHA (1951), KLIMA (1956), WALLWORK (1960), TARRAS-WAHLBERG (1961), MADGE (1964) and HAYES (1966) have shown the humidity and/or temperature relationships of Oribatei to affect their choice of certain microhabitats in the soil profile. The feeding activity of Oribatei has also been shown to be an important factor in determining the distribution of certain species (VAN DER DRIFT, 1951 ; RIHA, 1951 ; WALLWORK 1958, 1959 ; HAYES, 1963 ; LUXTON 1964, 1966).

In this study information on some factors affecting the microdistribution of Oribatei was obtained using soil sections (ANDERSON and HEALEY, 1970). A particular advantage of these sections for studying the vertical distribution of certain arthropods, such as Acari, is that a finer subdivision of the profiles can be studied than is possible by dividing and extracting core samples. The distribution of the animals can also be related to specific stages in litter decomposition.

MATERIALS AND METHODS

The locality

This study was made on two dissimilar woodland soil types in Blean Woods National Nature Reserve, near Canterbury, Kent. One sampling area is in a stand in which sweet chestnut (*Castanea sativa* MILL.) dominates, coppiced 40-60 years ago, with a thin understory of younger and smaller beech trees (*Fagus sylvatica* L.). The leaf litter is fragmented during the course of one year so that a distinct litter layer is absent by the following autumn. The humus layer is compact, about 5 cm. in depth with mor-like characteristics, and showing a transition at a depth of 6-10 cm to a bleached alluvial sand layer, 35-40 cm deep, based on London clay with flints. The profile is weakly podzolized at the junction of the sand and clay horizons.

The second sampling area is in a dense stand of *Fagus sylvatica*, also coppiced approximately 40-60 years ago, with occasional small birch (*Betula pendula* ROTH.) and oak trees (*Quercus petraea* [MATTUSCHKA] LIEBL.), situated about 20 metres due north of the *Castanea* stand. The litter layer is less clearly defined from the humus than in the *Castanea* site but is present throughout the year. The humus is of a friable mull-like moder type, 3-7 cm in depth on London clay with flints. The clay shows a tendency to gley. Both sample areas have a complete absence of ground flora.

Fortnightly temperature readings were taken in the *Castanea* site using a maximum and minimum thermometer at the humus litter interface.

Preparation of soil sections

Details of these techniques are given in ANDERSON and HEALEY (1970).

1. *Sampling.*

Three samples, 10 × 10 × 6 cm deep, were taken every 28 days in each of the sites from a randomly selected area, placed in perforated zinc embedding cages and packed in an insulated container with CO_2 ice. The quick freezing of the samples in the field rapidly kills soil animals in their natural positions and prevents disturbance to the samples between the sampling site and the laboratory. Water content samples were taken immediately adjacent to each block, divided into the sub-horizons defined below and sealed in polythene bags. The samples were dried at 100°C and the water content expressed as the percentage of wet weight. Samples were also taken similarly every 3 months, and pH measurements made on the separate sub-horizons. The pH did not change significantly in each sub-horizon over the period of study.

2. *Embedding, curing and sectioning.*

A vacuum embedding technique was employed to embed the sample in 20 p. 100 w/v gelatin. The gelatin is cured in 10 p. 100 formaldehyde and the blocks cut into 20 sections, each 5 mm thick.

3. *Analysis of the sections.*

The sections are flooded with water and scanned with a binocular microscope under intense two directional illumination. The depth of the sub-horizons, defined below, is measured in alternate sections. The depth of the litter layer is expressed as the mean sectioned leaves per section face.

RESULTS

The following sub-horizons of the A horizon are usually recognizable in samples of 5-6 cm depth :

Sub-horizon notation	Brief morphological description	Sub-horizon mean annual depth/section face (± 95 % limits)	
		Castanea	*Fagus*
A_0 *	Whole leaves showing little sign of feeding activity	3.5 (± 7.2) leaves	10.8 (± 8.2) leaves
A_{F_1}	Fragmented leaves, showing feeding by soil animals, with fæcal material	4.7 (± 6.7) mm	3.9 (± 6.8) mm
A_{F_2}	Finely fragmented plant material with heavy fæcal deposits, raw humus and mycorrhiza	11.6 (± 8.7) mm	12.8 (± 8.9) mm
A_{H_1}	Humus but with some recognizable plant material	22.9 (± 8.0) mm	19.8 (± 15.1) mm
A_{H_2}	Clay-humus complex with pellets of clay in the *Fagus* samples . . . . Humus/bleached sand transition zone in *Castanea* samples (A_{H_1} — A*e*)	12.6 (± 14.0) mm	16.7 (± 22.0) mm

The A_0 and A_{F_1} sub-horizons are classified as litter layers, the A_{F_2} and A_H sub-horizons as humus layers. Raw humus is considered as an intermediate stage in litter decomposition to humus, and is derived from disintegrated fæcal material further broken down by the activity of the microflora and fauna.

The gross morphological differences between the two profiles can be seen in fig. 1 and 2. These sections are not of the same sampling date but have been chosen as being characteristic of the two profiles.

The clear demarcation between the litter and compact humus layers in the *Castanea* profile (fig. 1) persists over the whole year. This is particularly due to the absence of burrowing earthworms (*Lumbricus rubellus* HOFF. is present in both sites but is limited to the litter and raw humus subhorizons). The *Castanea* humus is characterized by the droppings of Oribatei and Enchytraeidae. *Castanea* leaves are larger than those of other woodland deciduous trees and when wet lie matted together, flat on the A_F sub-horizons. The litter layer remains physically stable in this condition until the water content of the leaves falls below about 25 p. 100 wet weight ; the leaves then curl, the litter layer becomes looser and is easily disturbed by wind.

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* A_0 should read A_{00} throughout.

The delicate leaves are rapidly fragmented under these conditions, particularly in summer and autumn when they become brittle when dry. The fragmented leaf material settles or is washed out of the A_0 litter layer into the A_F sub-horizons. The physical fragmentation processes are more important than the activity of the soil and litter fauna in the annual breakdown of the *Castanea* litter (ANDERSON, unpublished).

Fagus leaves are smaller and tougher than *Castanea* and are less damaged by desiccation and wind action. A small population of *Lumbricus terrestris* L. is present in the *Fagus* sampling area. This earthworm contributes significantly to the frag-

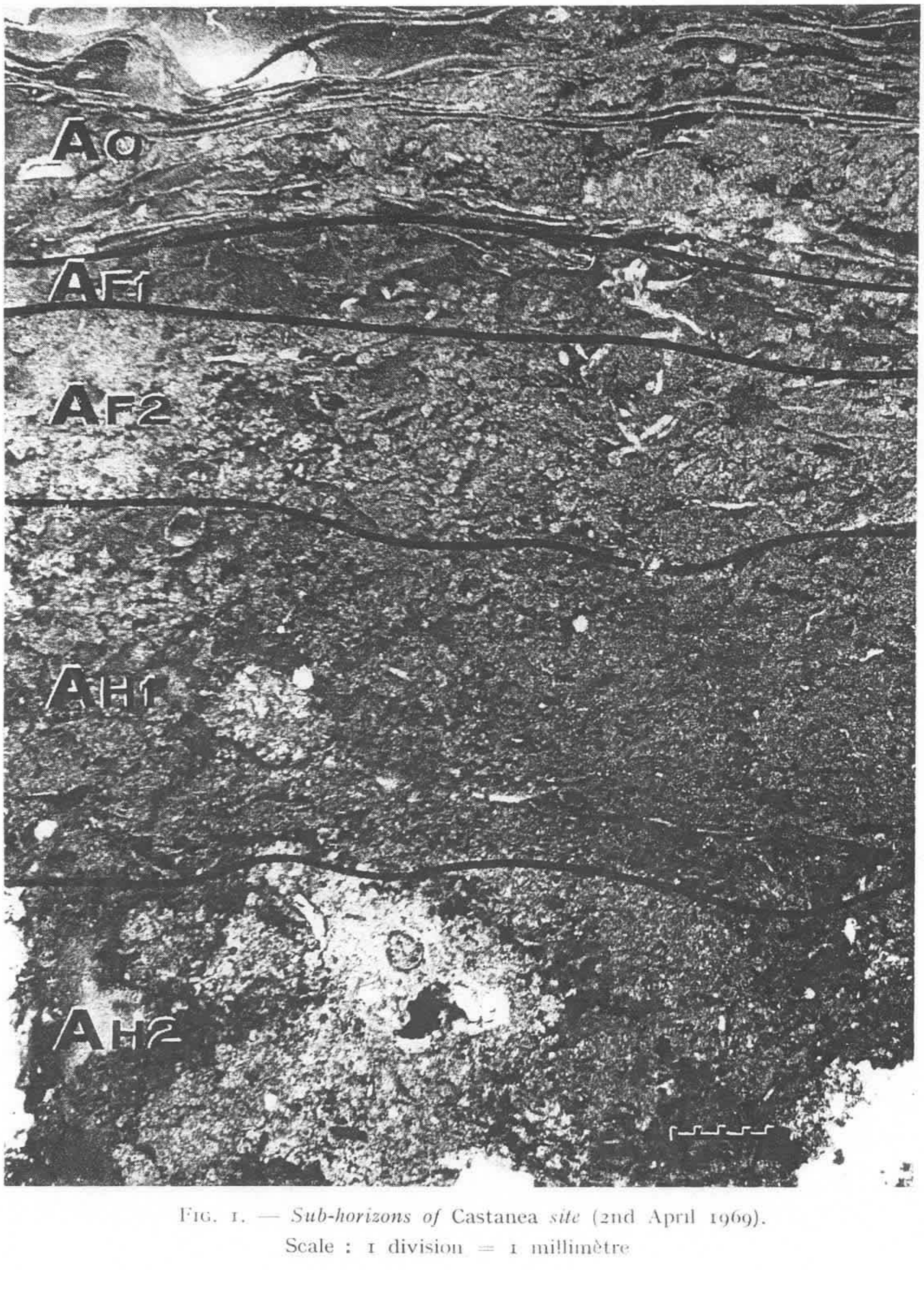


FIG. 1. — *Sub-horizons of* Castanea *site* (2nd April 1969).
Scale : 1 division = 1 millimètre

mentation of the leaf litter ; the appearance of the humus in figure 2 is attributable to earthworm burrowing activity. The humus layer has a looser structure than that of the *Castanea* site and clay mixed with organic material is redistributed throughout the section of the profile studied. The clay-humus complex assists in maintaining the stability of this open humus structure ; the sand and humus mixture in the lower A_{H_1} and A_{H_2} sub-horizons of the *Castanea* profile tends to become tightly packed with increasing depth as a result of the washing down of organic particles by rain water.

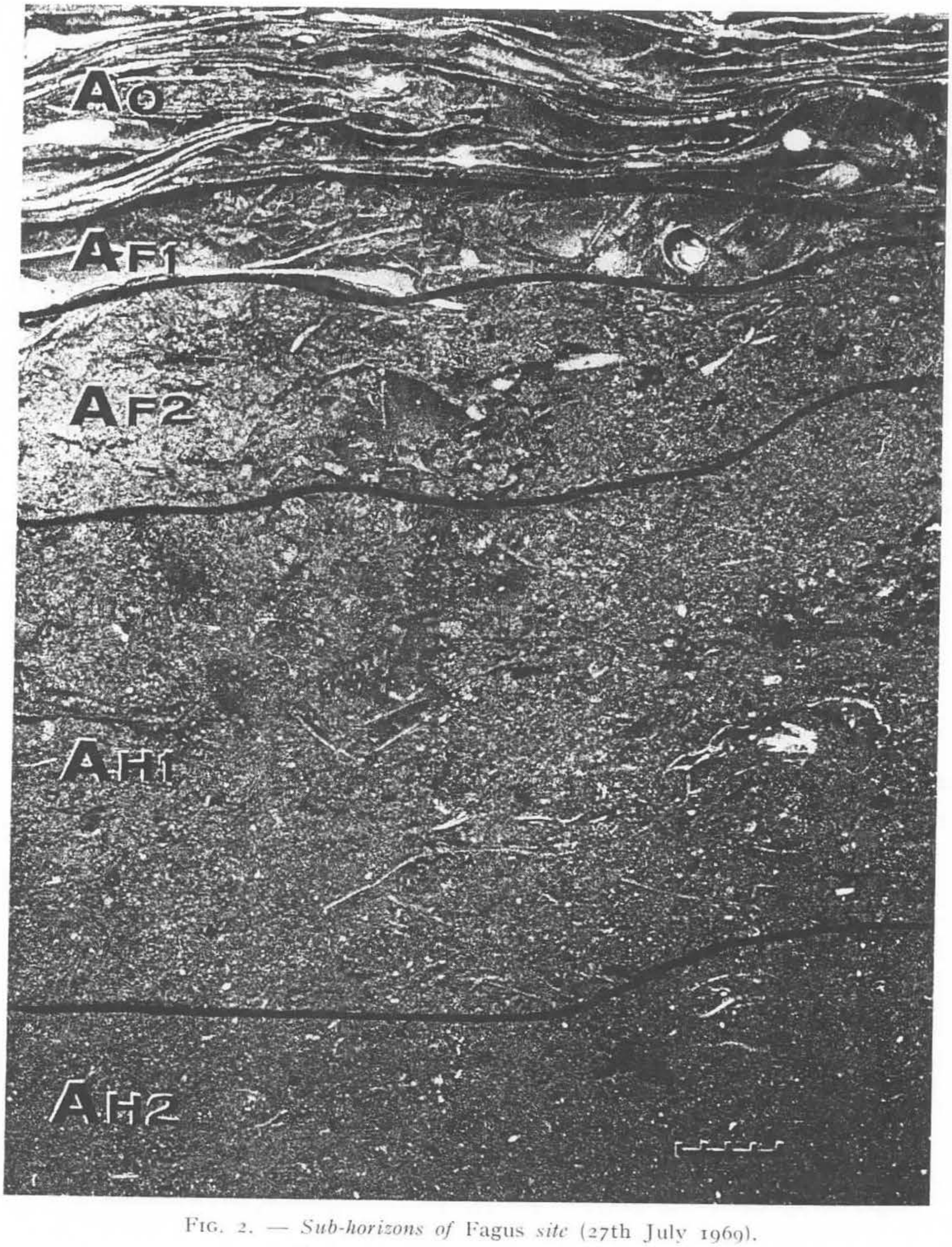
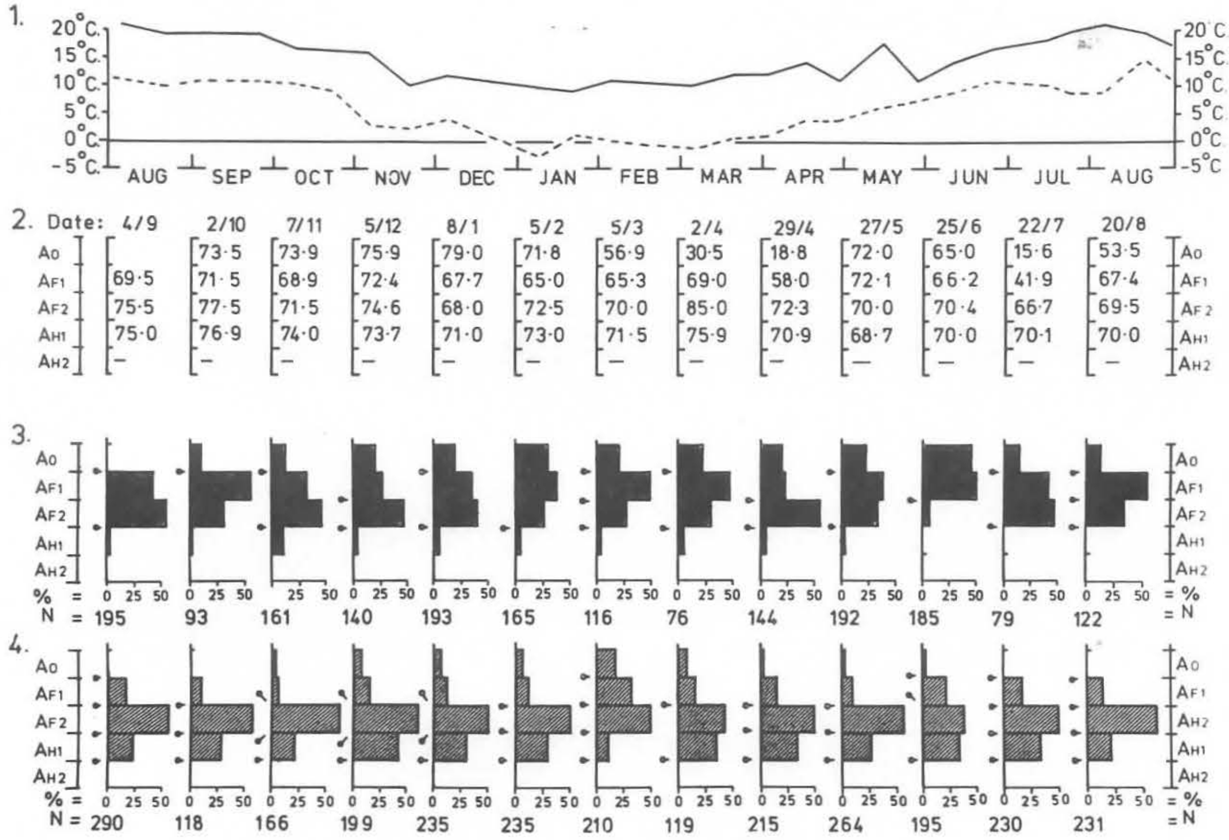


FIG. 2. — *Sub-horizons of* Fagus *site* (27th July 1969).
Scale : 1 division = 1 millimètre

Litter temperatures

The maximum and minimum A_{F_1} litter temperatures recorded in the *Castanea* site are given in figure 3 ; comparable data are not available for the *Fagus* site.



Date:	4/9	2/10	7/11	5/12	8/1	5/2	5/3	2/4	29/4	27/5	25/6	22/7	20/8
Ao		73·5	73·9	75·9	79·0	71·8	56·9	30·5	18·8	72·0	65·0	15·6	53·5
AF1	69·5	71·5	68·9	72·4	67·7	65·0	65·3	69·0	58·0	72·1	66·2	41·9	67·4
AF2	75·5	77·5	71·5	74·6	68·0	72·5	70·0	85·0	72·3	70·0	70·4	66·7	69·5
AH1	75·0	76·9	74·0	73·7	71·0	73·0	71·5	75·9	70·9	68·7	70·0	70·1	70·0
AH2	–	–	–	–	–	–	–	–	–	–	–	–	–

FIG. 3. — *Seasonal distribution of Oribatei in* Castanea *site*

(1) Maximum ——— and minimum - - - - - - - temperatures recorded at litter/humus interface.

(2) Percentage water content of sub-horizons (p. 100 wet wt.).

(3) Vertical distribution of adult Oribatei.

(4) Vertical distribution of juvenile Oribatei.

Note : The number of mites present in each sub-horizon has been expressed as a percentage of the total population (N). Pointers indicate where the percentages of mites in two adjacent sub-horizons differ significantly at the 95 p. 100 confidence level.

Sub-horizon water content

Water contents are given for the *Castanea* site in figure 3 (2) and for the *Fagus* site in figure 4 (1). Data have not been presented for the A_{H_2} sub-horizons as the mineral content at these levels produced erroneously low figures. Owing to the disturbance of the *Fagus* profile high mineral contents also affected the values made of the A_{H_1} sub-horizon ; the low A_{H_1} water content for January and February 1968 is clearly not related to desiccation of the profile. Since the termination of this study I have found that the subtraction of the ash content of the samples from their original wet weights makes a correction for mineral content, reduces variance by a factor of one or two decimal places and provides comparable water content values for the sub-horizons of both sites.

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Date:	4/9	2/10	7/11	5/12	8/1	5/2	5/3	2/4	29/4	27/5	25/6	22/7	20/8	
Ao	76·7	77·9	67·5	68·9	77·2	72·8	76·1	25·0	30·3	77·8	71·9	18·3	60·5	Ao
AF1	74·2	70·2	72·1	76·7	77·8	70·9	76·9	70·7	78·6	80·0	70·8	36·8	72·8	AF1
AF2	75·6	72·5	78·4	74·5	65·4	74·7	70·5	74·2	66·8	77·8	72·0	47·7	67·0	AF2
AH1	55·7	46·8	77·8	—	29·4	38·9	72·5	—	—	—	—	45·5	52·2	AH1
AH2	—	—	—	—	—	—	—	—	—	—	—	—	—	AH2

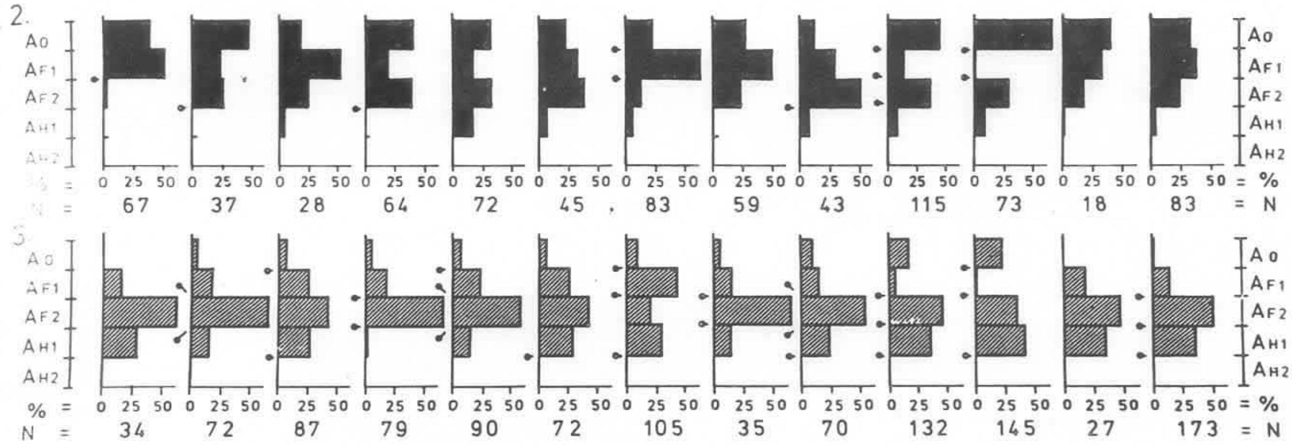

FIG. 4. — *Seasonal distribution of Oribatei in* Fagus *site*

(1) Percentage water content of sub-horizons (p. 100 wet wt.)
(2) Vertical distribution of adult Oribatei.
(3) Vertical distribution of juvenile Oribatei.

See note on fig. 3.

Vertical distribution of Oribatei

Parametric statistics are unsuitable for the analysis of the distribution of Oribatei in this study due to the small number of samples taken on each sampling date. The numbers of mites observed in each sub-horizon of the 3 samples have been expressed as a percentage of the total population (N). The 95 p. 100 confidence limits for this proportion were determined using the binomial function given by BAILEY (1959).

Seasonal variations in the proportions of adult and juvenile Oribatei for the two sites are given in figures 3 and 4. There was an increase in the adult and juvenile Oribatei in the *Castanea* Ao litter from September to November, reaching a maximum proportion of 20-25 p. 100 of the total population after the main period of litter fall in the last two weeks of October. This proportion remained constant until the end of June when the population showed a significant increase, followed by a sharp reduction in numbers during July and August. The population decrease in July may be related both to the low water contents of the A_0 and A_{F_1} sub-horizons, and to the physical instability of the litter layers when dry. The Ao litter mite populations did not show a proportional increase in August after the dry conditions in July despite the higher water content of the litter. This was partly due to the reduction in depth of this sub-horizon by litter fragmentation during the dry summer months. The depth of the A_{F_1} sub-horizon increased over the same period and there was an upward movement of the adult mites into this layer in August. High levels of litter feeding activity by soil organisms, particularly Diplopoda and Isopoda, occurred in the A_0 and A_{F_1} sub-horizons during August and September. This was associated both with high population levels of many arthropods in late summer and autumn, and also with the improved palatability of litter which had weathered and been subject to microbiological decomposition for 8 or 9 months. Juvenile Oribatei were absent from the A_{H_2} sub-horizon ; during the year of study four *Rhysotritia ardua* (C. L. KOCH) found burrowing in dead roots were the only adult Oribatei at this level. Juvenile Oribatei showed higher proportional levels in the A_{F_1} and A_{H_1} sub-horizons than the adults at all times of the year.

The distribution of Oribatei in the *Fagus* sections (fig. 4) was essentially similar to those from the *Castanea* site. Litter was present throughout the year, but decreased steadily from May/June to a mean depth of only two or three leaves in September 1968. These weathered leaves were classified as belonging to the A_{F_1} sub-horizon when covered with freshly fallen leaves in November. This classification affects only the representation of the distribution on October 1968 when the new litter layer was two or three leaves deep ; the populations of juvenile and adult Oribatei shown for the A_0 sub-horizon were present in the litter from the previous year. In November these animals are considered as occurring in the A_{F_1} sub-horizon ; the adult Oribatei in the new litter layer showed a rapid increase to a similar proportional level as that found in the *Castanea* A_0 litter. The low adult and juvenile A_{F_1} population

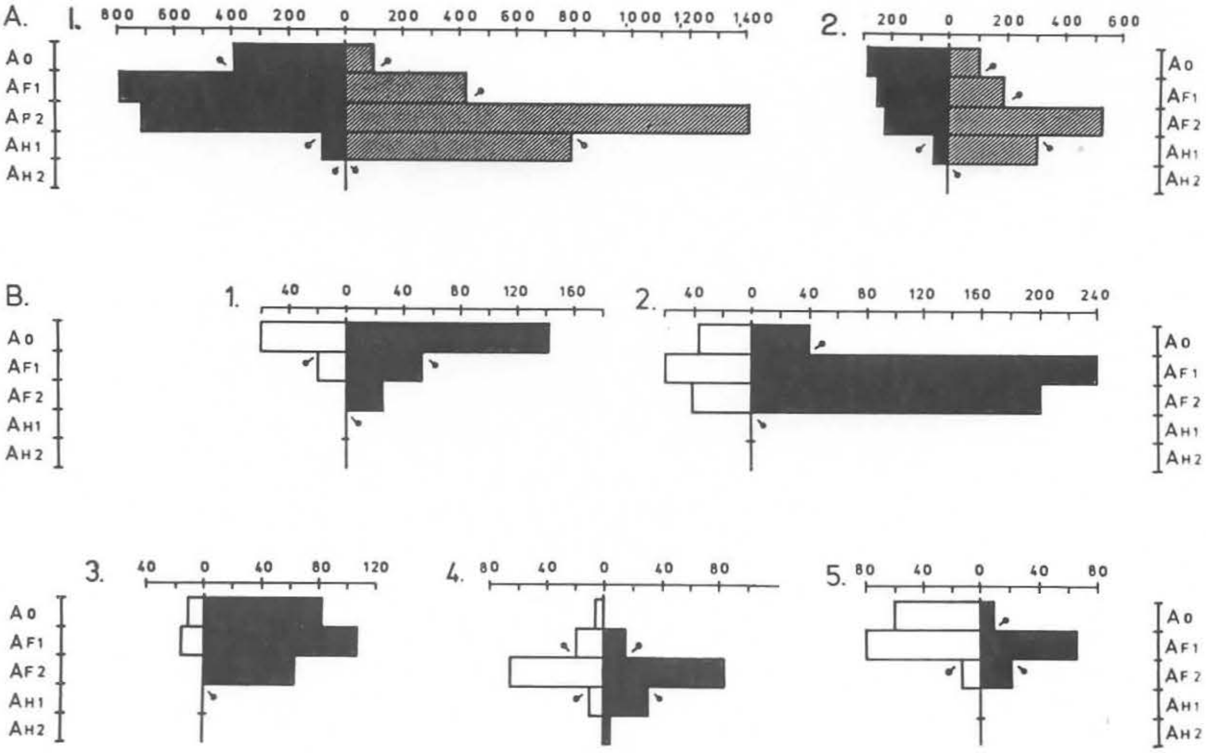

FIG. 5. — A. *Annual totals of adult and juvenile Oribatei in the* Castanea (1) and *Fagus* (2) sampling sites (780 section faces/site). Adults are shown in black, juveniles in grey.

B. *Annual totals of dominant adult Oribatei species in the* Castanea (black) *and* Fagus (white) *sampling areas.*

(1) *Carabodes labyrinthicus*
(2) *Nanhermannia elegantula*
(3) *Hermaniella granulata*
(4) *Rhysotritia ardua*
(5) *Steganacarus magnus*

NOTE : Pointers indicate where the percentages of mites in two adjacent sub-horizons differ significantly at the 95 p. 100 level.

levels shown for May and June 1969 are obscured by the difficulty of defining that sub-horizon at those times of the year. The juvenile Oribatei had a similar seasonal distribution pattern to those in the *Castanea* profile despite the different size of the populations observed. The fluctuations in the proportion of the juvenile populations in the A_{H_1} sub-horizon reflected the heterogeneity in the mineral content of the *Fagus* humus.

The annual totals of adult and juvenile Oribatei in both sites (780 sections/sampling area) are given in figure 5 (A). Most of the adult mites in both sites occurred in the litter and raw humus sub-horizons. The total *Castanea* population was approximately three times that in the *Fagus*. The raw humus (A_{F_2}) and humus (A_{H_1}) sub-horizons of the *Castanea* site are made up of finely divided, compact and decomposed plant material and a large proportion of the juvenile Oribatei, particularly the early stages, was found in cavities in the humus excavated by their feeding activity. The stable water contents of the sub-horizons and the high calorific content of the humus material (5.07 cal/g ash-free oven-dry weight with low mineral content compared to the mixed *Fagus* humus) may have formed an ideal micro-habitat for the development of juvenile Oribatei. In addition, the humus layers show small and gradual temperature fluctuations and the adoption of an endophagous microhabitat will reduce juvenile mortality from arthropod predators, such as the Mesostigmata (Acarina). In the *Fagus* site the A_{F_2} and A_{H_1} humus sub-horizons have a looser structure and higher mineral content due to the burrowing activity of earthworms. The humus material may have been not only less suitable for the endophagous development of the juveniles but the looser structure of the humus may have resulted in higher mortality due to predators. The state of decomposition of the leaf lamellae, petioles and raw humus suitable for the endophagous development of certain juvenile Oribatei, also meets the palatability requirements of the earthworms. The ingestion of juvenile stages by *Lumbricus terrestris* may have contributed significantly to the factors limiting the size of the Oribatei population in the *Fagus* sampling area.

Approximately 70 p. 100 of the adult populations observed in the sections from both sites were composed of *Carabodes labyrinthicus* (MICH.), *Nanhermannia elegantula* BERL., *Hermanniella granulata* (NIC.), *Steganacarus magnus* (NIC.) and *Rhysotritia ardua* (C. L. KOCH). The annual totals of these species are given in figure 5 (B) and their seasonal distribution in the *Castanea* site in figure 6. The *Fagus* populations were too small to make a valid seasonal comparison.

Carabodes labyrinthicus.

C. labyrinthicus [fig. 6 (1)[showed an upward redistribution of adults during the autumn months when the raw A_0 litter layer was deposited. The movement of the population into the freshly fallen litter may have been associated with the development of the fungal flora ; gut analysis of specimens removed from the sections indicated that this species was feeding predominantly on fungal hyphae during this period. Most of the population remained in the A_0 sub-horizon from December until July. There was no downward redistribution of the population during the winter period or in response to the relatively dry conditions during April. The reduction of the A_0 litter population of *C. labyrinthicus* in July may have been associated with the physical instability of the dry litter or with the dessication of food substance.

The latter factor could influence the distribution of the population at temperatures far below the upper limits of the tolerance range.

The total numbers of *C. labyrinthicus* observed in the sections from both sites are given in figure 5 (B 1). It can be seen that this species was significantly associated with the A_0 litter in both sites.

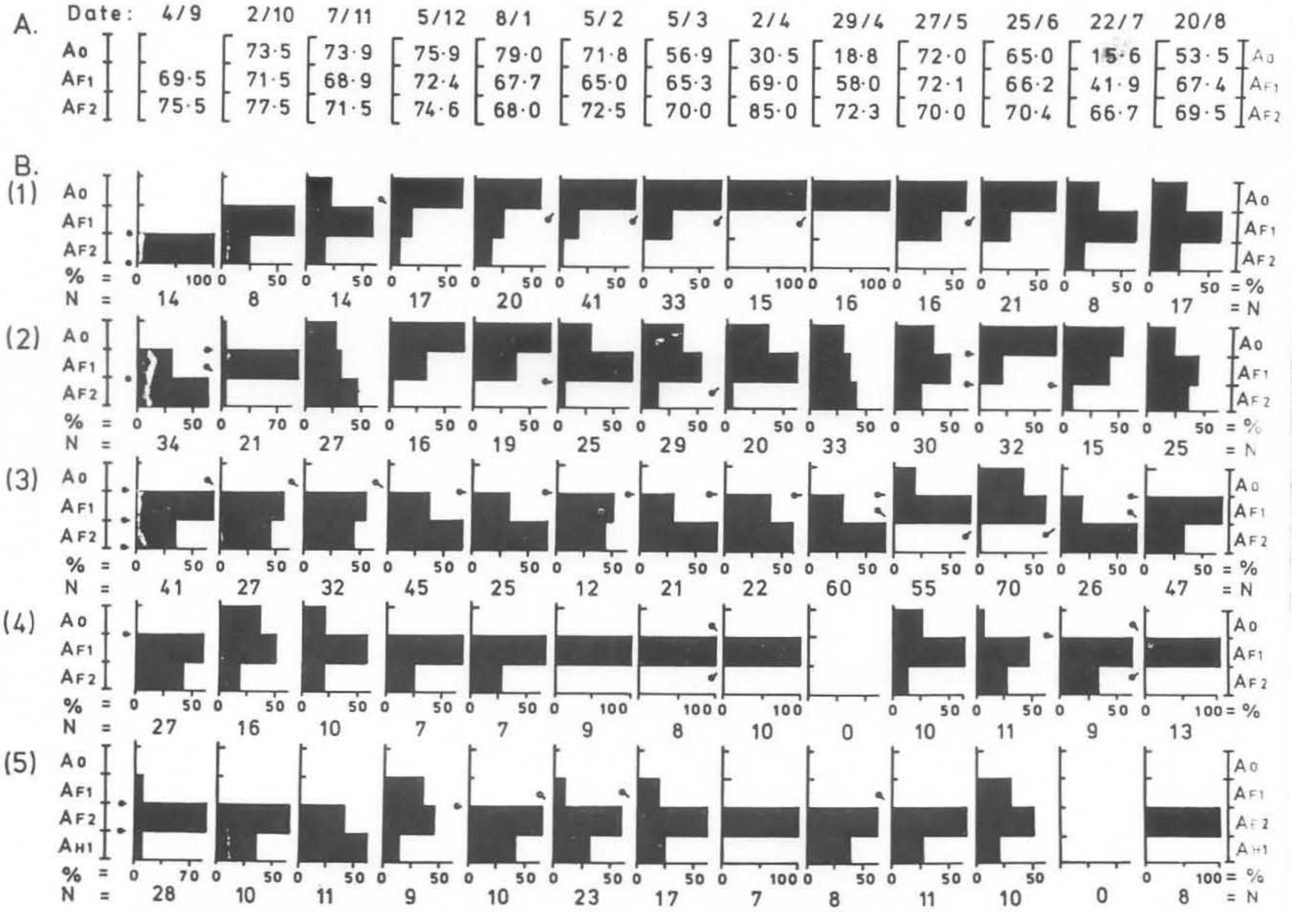

FIG. 6. — *Seasonal distribution of dominant adult Oribatei in the* Castanea *sampling site*

A. Water contents of sub-horizons

B. (1) *Carabodes labyrinthicus*
(2) *Hermanniella granulata*
(3) *Nanhermannia elegantula*
(4) *Steganacarus magnus*
(5) *Rhysotritia ardua*

See note on fig. 3.

Hermanniella granulata.

H. granulata showed an irregular distribution in the seasonal [fig. 5 (B 3)] and annual totals [fig. 6 (B 2)] apparently unrelated to temperature or to dry litter conditions. The vertical distribution of this species was obscured by the frequent occurrence of *H. granulata* in cryptic microhabitats, particularly in tunnels made in rotten wood by *Cylindroiulus punctatus* (LEACH) [*Diplopoda, Julidae*]. A large number of the late nymphal stages was found in decayed wood ; some individuals may reach maturity under these conditions and emerge to take up a free living existence in the litter. Nymphs were also found tunnelling in the compact masses of raw humus and the fæcal masses of Diplopoda. *H. granulata* was absent from the *Castanea* A_1

sub-horizons. The low population levels in the *Fagus* site may be related to the palatibility of *Fagus* leaves, as this species was found to feed primarily on *Castanea* leaf material in various stages of decomposition, also on wood, fungal hyphae and *Pleurococcus*, or to the less frequent occurrence of suitably decomposed wood for the development of the juvenile stages. The disturbance of the profile by earthworms may also be a factor contributing to the diferences in population size.

Nanhermannia elegantula.

The seasonal distribution of *N. elegantula* [fig. 6 (B 3)] showed a downward movement from the A_{F_1} sub-horizon in September to the A_{F_2} from December to April. The differences between the A_{F_1} and A_{F_2} populations are significant at the 90 p. 100 confidence level and may represent a redistribution brought about by the low winter temperatures given in figure 3 (A). In May and June there was a significant upward redistribution into the A_{F_1} and A_0 litter sub-horizons, while the A_{F_2} populations decreased to a low level. Gut content analysis indicated that this species was feeding on litter in advanced stages of decomposition, characteristic of the A_F sub-horizons, or possibly on faecal material of soil animals. The A_0 litter may have been sufficiently decomposed by May and June to have been palatable to this species but the gut contents of mites feeding on the faeces of Enchytraeidae and *Lumbricus rubellus* present in the A_0 litter would appear similar. During the dry period in July most of the population moved out of the litter sub-horizons into the more humid A_{F_2} layer.

Steganacarus magnus.

The seasonal distribution of *S. magnus* is given in figure 6 (B 4). This species was associated with the fragmented *Castanea* and *Fagus* litter (A_{F_1}) throughout the study. The higher proportion of *S. magnus* in the A_0 litter of the *Fagus* sections than in those from the *Castanea* site may be attributable to the presence of *Fagus* litter throughout the year, while the depth of the *Castanea* litter was reduced during the summer and autumn months. *S. magnus* was found infrequently in the A_{F_2} sub-horizons and was absent from the A_H sub-horizons of both sites. Tritonymphs were frequently found in rotten wood in the A_F sub-horizons of both sites. The populations observed in the sections of each sampling date are too small to discuss seasonal redistribution in relation to temperature and soil water content. Gut contents contained mainly leaf mesophyll in a relatively undecomposed state, but wood and fungal hyphae were also found.

Rhysotritia ardua.

The seasonal distribution of *R. ardua* [fig. 6 (B 5)] indicates that this species was associated with the A_{F_2} raw humus layer at all times of the year. No significant redistribution patterns were shown by this species. Small numbers were found burrowing in the A_{H_1} sub-horizon, particularly in wood in advanced stages of decomposition and occasionally in decayed roots to the full depth of the sections. *R. ardua* was never observed in the *Castanea* A_0 litter; a small number of adults were recorded in deep A_0 *Fagus* litter pockets [fig. 5 (B 4)] but occurred in the A_{F_1} litter of both sites. A number of adults were found in rotten wood and twigs in the A_F sub-horizons of both sites. Few juvenile stages were recognized in the sections; tritonymphs were observed either in rotten wood, or burrowing in the A_{F_2} and A_{H_1} humus sub-horizons

Gut content analyses of this species indicated feeding on finely divided raw humus and the dark fungal hyphae associated with mycorrhiza.

DISCUSSION

The proportion of the total population of adult and juvenile Oribatei present in the A_0 litter sub-horizons of both sites during the winter and spring months does not show statistically significant fluctuations despite temperatures as low as — 2.5°C recorded beneath the A_0 litter layer of the *Castanea* site [fig. 3 (1)]. These results are in marked contrast to the studies of Riha (1951), Van Der Drift (1951), Wallwork (1959), Tarras-Wahlberg (1961) and others, who have described a seasonal redistribution of Oribatei, particularly the adults, from the litter to the humus layers in response to winter temperatures, as well as to high summer temperatures usually associated with the desiccation of the surface layers of the profile. Van Der Drift (1951) and Karppinen (1955) have attributed this downward movement to an avoidance of the dry, cold conditions which can exist in the litter at this time. In support of this view, Riha (1951) has shown that the desiccation tolerance of many Oribatei decreases rapidly below 7°C. The relatively stable population present in the litter in this study may be due to the constancy of the water content of the litter or to the milder winter conditions than those which may have existed during the studies cited. Wallwork (1959) gives the mean winter litter temperature in his hemlock-mor site (Michigan, U. S. A.) as 0°C, which is 5°C below the mean temperature recorded in the litter at Blean ; relevant litter temperature data from the other studies are not available for comparison. Sengbusch (1951), Wallwork (1959) and Tarras-Wahlberg (1961), however, have shown juvenile Oribatei to survive frozen conditions in the litter layer while Haarløv (1942) and Lebrun (1964) failed to observe a winter redistribution of adult Oribatei. The contradictions in these reports emphasise that seasonal trends in the vertical distribution of total adult and juvenile Oribatei may be obscured by the physiological tolerances and behaviour patterns of the individual species and their interaction with the physical characteristics of the area studied.

The A_0 litter layer is subject to more rapid fluctuations and extremes of temperature and humidity than the other sub-horizons. *Carabodes labyrinthicus* had a characteristic distribution in this litter layer and has been described by Riha (1951), Tarras-Wahlberg (1961) and Madge (1965) as tolerant of xeric conditions and higher temperatures than many other mites (Madge, 1964). A mite of this size (500 × 300 μ) can probably find humid microclimates in the general fæcal material present between tightly packed leaves during dry periods. Van Heerdt (1950) has shown that the hygroscopic properties of dead leaves provide high humidities for longer than expected under dry conditions. *C. labyrinthicus* moves out of the litter when the leaves become loose and unstable.

Riha (1951), Hartenstein (1962) and Madge (1965) have described *Carabodes* spp. as being primarily fungivorous. This is supported by the findings in this study though small quantities of highly decomposed organic material were found in guts, analyzed during late summer and autumn. HARTENSTEIN (1962) and LUXTON (1966) show some Oribatei to be highly selective in their feeding and LUXTON also suggested this to be a contributing factor in the zonal distribution of Oribatei in a salt marsh. The distribution of *Carabodes labyrinthicus* in this study may reflect selective feeding on one or more species of fungi characteristic of the A_0 litter layer in both sites.

Hermanniella granulata is moderately resistant to low humidities (RIHA, 1951) but was found in rotten wood and twigs during dry periods in the litter. These microhabitats are physically stable and retain high levels of moisture longer than the leaf litter. Rhia also described *H. granulata* as feeding on damp litter ; however, the individuals present in the comparatively undecomposed litter in spring may feed on faecal material containing high fungal and bacterial populations.

Nanhermannia elegantula occurs in the A_F sub-horizons over most of the year. RIHA (1951) and VAN DER DRIFT (1951) suggest that this species has a low tolerance of dry conditions. MADGE (1964) has shown that *Nanhermannia* spp. do not have the waxy cuticle present in most adult Oribatei and are subject to rapid water loss in low relative humidities. It might be expected that *N. elegantula* would occasionally be found in the A_{H_1} humus layer as it is sufficiently small (600×270 μ) to move through pores in the humus and was frequently found in confined microhabitats in the raw humus of the A_{F_2} sub-horizon. However, the complete absence of this mite from the A_H humus layers suggests that food may be an important factor in determining its distribution.

The annual totals of *Steganacarus magnus* and *Rhysotritia ardua* in the two sites [fig. 5 (B 4) and (B 5)] show that these species were associated with the A_{F_1} and A_{F_2} sub-horizons respectively. HAYES (1966) found *S. magnus* more tolerant of low humidities than *R. ardua* and this may contribute to the differences in the depth distribution of these two species. However TODD (1949) has shown that the relative humidity of the lower litter layers rarely falls below 80-90 p. 100 throughout the year and it seems likely, in view of the small spatial separation of the A_{F_1} and A_{F_2} sub-horizons, that the distribution is related to feeding preferences rather than to temperature or humidity gradients.

HAARLØV (1953) has suggested that the decreasing diameter of soil cavities with increasing depth may limit the downward distribution of soil Acari. This could be a reasonable interpretation of the distribution of the Oribatei in the *Castanea* site [fig. 5 (A 1)] where the A_{H_1} humus is compact. The adults predominantly occur in the looser A_0 and A_F sub-horizons, while the smaller juvenile stages are also present in high numbers in the humus. However, despite the looser structure of the *Fagus* humus, the vertical distributions of total adult and juvenile Oribatei and the individual species studied (fig. 5) show a high degree of similarity in both sites. These similarities in distribution are due to the division of the soil profile into sub-horizons defined in terms of the morphological character of certain major stages in the decomposition of leaf litter. It would appear that the vertical distribution of Oribatei in both sites is governed more by the selection of certain food materials characteristic of these sub-horizons than by the physical characteristics of their environment.

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RÉSUMÉ

OBSERVATIONS SUR LA DISTRIBUTION VERTICALE DES ORIBATES (*ACARINA*) DANS DEUX SOLS FORESTIERS

On a étudié, en utilisant des sections de sol, la distribution verticale des oribates dans deux boisements présentant des types différents de litière et d'humus. On a défini les sous-horizons des profils du sol d'après les caractères morphologiques de la matière végétale en décomposition. On a mis en parallèle, d'une part, la distribution saisonnière des oribates totaux (adultes et juvéniles), ainsi que des adultes de cinq espèces individuelles et, d'autre part, la température, la teneur en eau des sous-horizons et le comportement alimentaire. Certaines espèces ont un type de distribution verticale spécifique ; celui-ci est resté constant tout au long de l'année de la présente étude ; on a mis en évidence la relation entre ce phénomène et le comportement alimentaire de chaque espèce.

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DISCUSSION

M. MALDAGUE : Vous mentionnez une valeur calorique de 5.07 cal/g dans l'horizon humique. Auriez-vous des chiffres pour la litière ?

Et pourriez-vous expliquer la raison de la valeur plus élevée obtenue dans l'horizon humique ? J'ai observé des valeurs analogues dans certaines érablières à sucre (*Acer saccharum)*.

J. M. ANDERSON : The humus horizon contains predominantly decomposition resistant leaf components, such as lignins, which have high calorific values. The juvenile Oribatei are unlikely to be digesting these materials but are probably feeding on heterotrophic microorganisms.

J. VAN DER DRIFT : Compliments for these fine results with this new technique giving insight in the real microdistribution of the microarthropods.

What about perspectives of this technique for collemboles and enchytraeides ?

J. M. ANDERSON : Thank you. Both *Collembola* and *Enchytraeidae* are reasonably well preserved in the sections, though not as well as the Acari. Unfortunately the early juvenile stages of Collembola are difficult to see. I have not attempted a detailed investigation of enchytraeid distribution but there might be difficulties in view of the body length of these animals.

N. HAARLOV : 1° It would interest me to hear how it is possible to count all specimens in a section. The animals may be covered by plant debris, humus etc. and thus be difficult to observe.

2° Can you explain why *Carabodes labyrinthicus* is mainly found in the A_0 layer even if the humidity level here is rather low ? Do you think the mites are attracted by the light ? Some structures in the cuticle might perhaps be interpreted in that way.

J. M. ANDERSON : This is a good point and one that is particularly important in respect of the statistical treatment of data obtained from the sections. Only mites exposed on the face of the sections were recorded otherwise higher subjective estimates of mite numbers would be obtained for the open structured litter layers than for the more compact humus layers.

I have suggested that the position of *Carabodes labyrinthicus* in the A_0 litter is maintained by its physiological characteristics and its fungal feeding habits, possibly on species characteristics of this level in the profile. Other factors may well be involved including light sensitivity, but these are aspects I have not invetigated.

P. LEBRUN : Vous avez mis en évidence une grande spécificité dans la distribution verticale des Oribates adultes. Suite à vos conclusions, pouvez-vous répondre aux deux questions :

1° Est-ce qu'on retrouve la même spécificité pour les immatures ?

2°. Est-ce que, pour une même espèce, les adultes et les immatures ont une distribution verticale semblable ?

J. M. ANDERSON : I have not yet attempted the specific identification of juvenile stages, but it appears that tritonymphs of these species are found at a similar level in the profile as the adults. I have not made any analyses of the gut contents of juvenile Oribatei.

P. W. MURPHY : The author has pointed out that the numbers of small oribatid mites could not be readily counted using his sectioning technique. There are a number of other small animals such as members of the Hypochthoniidae which could be overlooked for similar reasons. Were separate extractions carried out to determine the species composition of the sites ? In regard to the vertical distribution of the mites and arising from the comments of M. Lebrun, we have found distinct differences in the distribution of adults and juveniles of *Platynothrus peltifer* in oak woodland. During winter the juveniles occur closer to the surface of the litter layer, the adults occuring somewhat deeper in the same layer.

J. M. ANDERSON : Small, poorly pigmented mites, including the juvenile stages, can be fairly easily seen in the sections but it is the small dark species such as *Oppia* which are the most difficult to find. Extractions were not made during the study period to independantly determine species composition or population fluctuations. I was only investigating the vertical distribution of the five dominant species and not their population dynamics using this method. However it was interesting to find that the density estimates of juvenile oribatides determined independantly using high gradient extraction methods were substantially lower than the estimates obtained from the sections. This was particularly true of the *Pthiracaridae* and larvae. This was due to the endophagous habit of many oribatides encountered in the sections. I think that many of these animals would not be able to escape from these microhabitats before the sample becomes dessiccated in an extractor.

G. W. YEATES : I would like to comment on your ideas on vertical distribution of Oribatei and its relationship to the diameter of soil cavities. JONES, LARBEY and PARROTT have recently suggested that soil nematodes tend to decrease in size with increasing depth due to decrease in the diameter of soil pores. In work at the Danish I. B. P. Hestehave beech forest site I am collecting data on the dimensions of the soil nematodes. Each month 500 individuals from each of the litter, 0-3 cm mineral soil and 3-6 cm soil are measured. The grain size distribution in both soil layers is similar but the porosity of the 0-3 cm layer is about 60 p. 100 and that of the 3-6 cm layer about 50 p. 100. The differences in mean dimensions and biomass between the layers are often significant at the 95 p. 100 level, but the layer in which the mean is greatest varies from month to month. In addition to probable changes in distribution of food for the nematode fauna, whose specific composition and thus feeding preference is variable from month to month, I wonder whether variation in the composition of the soil air is a significant factor, either for nemaodes, Oribatei or the soil micro- and mesofauna as a whole. This may be more important for the « aquatic » forms.

J. M. ANDERSON : Quite honestly I do not know. I have not made any determinations of CO_2 or O_2 concentrations in soil interstices. This might well be important for some soil animals but, for example, certain astigmatid mites are exceptionally tolerant of both low O_2 levels and high CO_2 concentrations in the soil. The distribution of soil animals will obviously be determinea by the interaction of a large number of continuous variables, though I think food substances may be particularly important.

M. S. GHILAROV : I would like to mention that many investigations on seasonal variations of vertical distribution of Oribatids are carried out in the U. S. S. R. Publications by L. SITNIKOVA, D. KRIVOLUTSKY, E. SHALDYBINA, L. GOLOSOVA may be mentioned. Russian authors studied the vertical distribution down to 100-180 cm. Even in humid spruce forests in Moscow Region Oribatids penetrate in winter, down to 120 cm. Dr KRIVOLUTSKY : Who is present here, may give precise bibliographical Russian data concerning the problem under discussion.

J. M. ANDERSON : Thank you for pointing out the work of your colleagues, perhaps you would introduce me to them after this session.

It is interesting that Oribatids have been found at these depths ; the humus horizon was very shallow at Blean and was therefore ideal for this study.

G. ZACHARIAE : For *Pseudotritia* (= *Rhysotritia*) *ardua* it was stated by FÜHRER (1958), that in his Austrian study area it was bound strictly to *Artemisia* roots. You found it feeding on weathered residues and humus substances. This shows that local findings must not be generalized at once, and that the distribution of these mites is not related to certain bacteria species but more likely to special chemical or physical properties of their substrate.

J. M. ANDERSON : Yes, I agree with you.